Variability of zooplankton communities over the Emperor Seamounts, Northwest Pacific

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Introduction

In the northwestern Pacific Ocean, most studies of zooplankton communities are focused on marginal seas, mainly due to the importance of ther biological resources (Hirota and Hasegawa, 1999; Radchenko et al., 2010b; Shuntov, 2001, 2016). We suggest to change the focus from well-studied zooplankton communities of the marginal seas to the study of communities in open deep-sea waters of the ocean. A unique combination of climatic, geological, and biological characteristics of the Northwest Pacific regions creates specific conditions in open−ocean ecosystems that distinguish them from those of marginal seas (Nesis, 1982; Ma et al., 1983; Vinogradov, 1997; Hu et al., 2015). Stocks of commercially valuable pelagic fishes (e.g., Japanese sardine *Sardinops melanostictus*, Pacific saury *Cololabis saira*, and Pacific chub mackerel *Scomber japonicus*) are concentrated in the open ocean waters (Kurita et al., 2004; Sugisaki and Kurita, 2004).

In the open western Pacific Ocean, the main studies of zooplankton communities were conducted in the subarctic (Yamaguchi et al., 2002; Chiba et al., 2006; Chiba et al., 2009) or in the tropical and subtropical regions (along 143°E, 146°E, 155°E and 160°E) (Zhang et al., 1995; Le Borgne et al., 2003; Nagai et al., 2015; Dai et al., 2016; Long et al., 2021). Compared to these numerous studies, relatively little information is available about the latitudinal changes in zooplankton communities in the transitional zone between the subarctic and subtropical regions, and the majority of these data are limited to the epipelagic zone (Yamaguchi et al., 2004; Matsuno and Yamaguchi, 2010; Yamaguchi et al., 2015; Sun et al., 2017). Consequently, the spatial heterogeneity of zooplankton of the western Pacific Ocean ecosystem is still poorly understood. Without understanding the processes in the pelagic zone, particularly in the changing transitional zone of the Pacific Ocean, where the distribution centers of subarctic and subtropical species are observed to shift, we cannot identify and predict changes in pelagic ecosystems. Most zooplankton species, having a short life cycle, show quick responses to environmental changes and are among the first to respond to climate changes (Chiba et al., 2006; Coyle et al., 2011; Eisner et al., 2014; Ershova et al., 2015).

This study was aimed to understand differences in zooplankton communities over vertical and horizontal gradients that represent different environmental variations between the "warm ocean" and the "cold ocean". This study provides the first description of the zooplankton species diversity, with an emphasis on the copepod taxa, along the Emperor Seamount Chain, Northwest Pacific, for which there has been little information to date (Fedosova, 1980). The lack of information about the structural and functional characteristics of zooplankton in this region may be a major obstacle for better understanding the specifics of a marine ecosystem and for harvesting pelagic fish, since it is known that the Emperor Seamounts are the site of the largest documented catches of fish and invertebrate compared to other waters over seamounts in the world (Darnitsky et al., 1984).

Materials and Methods

The study was based on 47 zooplankton samples collected by the R/V *Akademik M.A. Lavrentyev* over the Emperor Seamounts Chain in the Northwest Pacific in the area within the longitudes 170–171°E and the latitudes 34°–44°N from July 13 to August 11, 2019. Twenty nine stations were sampled in the areas over the Koko (171°E, 34°N), Jingu (171°E 38°N), Nintoku (170°E 40-41°N), and Suiko (170°E 44°N) guyots (Fig. 1). Sampling was performed during daylight or night hours by vertical tows of a WP2 net (opening diameter, 0.57 m; mesh size, 200 μm). For each station, the epipelagic (EZ) (0–200 m deeps) and mesopelagic zones (MZ) (200–800 to 1000 m deeps) were considered separately. The samples were fixed with a 4% formaldehyde solution. Simultaneously with sampling, hydrological data were measured at each station using a SBE 19 plus V2 SeaCAT CTD profiler from the surface to the depth of immersion. Processing of plankton samples was performed visually under a microscope (Lomo, MSP2), using the World Register of Marine Species (WoRMS Editorial Board, 2015). The zoogeographical structure of the fauna was divided into three major groups of species, which we categorized as follows: the Subtropical Pacific group, consisting only of tropical/subtropical origin species (e.g. *Candacia longimana, Corycaeus farranula*, *Eucalanus elongatus*, *Haloptilus acutifrons, and Oncaea media*); the Subarctic Pacific group, consisting only of boreal origin species (e.g. *Eucalanus bungii*, *Metridia pacifica*, *Neocalanus cristatus*, *N. plumchrus*); and the Widespread Pacific group, including species found in both subtropical and subarctic waters of the Pacific Ocean (Brodsky, 1957; Fedosova, 1980; Vinogradov, 1997; Razouls et al., 2005-2021).

We used the definitions of Favorite et al. (1976) and Saito et al. (2011) for the subarctic front (the 4°C isotherm at depths from 100 to 500 m) and the subarctic boundary (the 34.5 PSU isohaline in the upper 200 m layer) to distinguish three major domains: Subtropical Pacific (STP); Subarctic Pacific (SAP); and Transitional Pacific (TRP). Thus the SAP domain was north of the subarctic front (north of 42°N), the TRP domain was between the subarctic front and the subarctic boundary (between 38 and 41°N), and the STP domain was south of the subarctic boundary (south of 37°N).

The abundance and biomass of zooplankton were expressed as individuals per cubic meter (ind. m^{-3}) and milligram wet weight per cubic meter (mg WW m^{-3}), respectively. Shannon-Wiener diversity index (H') was calculated as following: $H' = -\Sigma pi \ln pi$, where H' is the Shannon–Wiener diversity index, pi is the proportion of the i^{th} taxa in the abundance matrix. To analyze similarities in the zooplankton communities among the stations and of the distribution pattern among the species, cluster analyses were made on a Bray-Curtis similarity index calculated from the log-transformed data of zooplankton abundance at each station. Non-parametric Spearman rank-order correlations were computed between selected univariate zooplankton characteristics (abundances and biomass of zooplankton and copepods species, numbers of copepod species of different zoogeographical group in surface, epipelagic and mesopelagic layers) and environmental variables. All described statistical analyses were performed using Past 4.05 software and Statistica 10 (StatSoft, Inc.). The significance level for all statistical tests used was $p < 0.05$. The map of sampling stations was created with ODV 4.

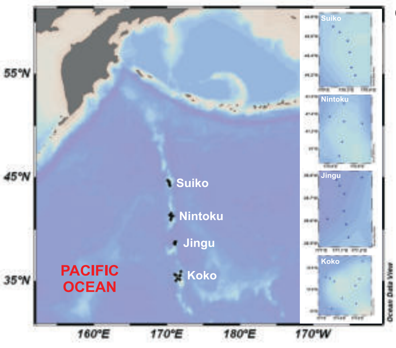

Fig. 1. Location of the sampling stations over the Emperor Seamounts within the area 170–171°E and 34°–44°N during July–August 2019.

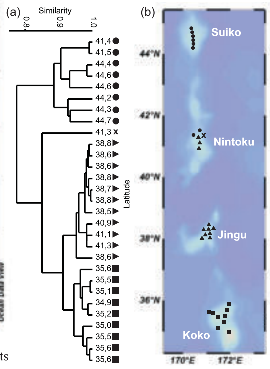

Fig. 3. Station similarities as determined by hierarchical clustering based on log-transformed zooplankton abundance (a) and spatial distribution of zooplankton community groups (b). Fill circle: Subarctic Pacific community; fill triangle: Transitional Pacific community; fill square: Subtropical Pacific community.

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Results and Conclusion

Abundance and biomass

The abundance of zooplankton ranged from 93.9 (at 35°N) to 1561.4 ind. m^{-3} (at 44°N), with an average value of 383.1±69.4 ind. m^{-3}. The biomass of zooplankton ranged from 34.5 (34°N) to 756.4 mg WW m^{-3} (44°N), with an average value of 126.1±35.1 mg WW m^{-3}. The average abundance and biomass in the three domains increased generally with latitude, STP < TRP < SAP. The abundance of zooplankton in the epipelagic zone ranged from 105.3 (35°N) to 1561.4 ind. m^{-3} (44°N), with an average value of 514.7±89.4 ind. m^{-3}. The abundance of zooplankton in the mesopelagic zone ranged from 93.9 (35°N) to 653.7 ind. m^{-3} (44°N), with an average value of 231.2±45.8 ind. m^{-3}. The average biomass in the epipelagic and mesopelagic zones of the STP domain (35.8±20.8 and 36.5±21.8 mg WW m^{-3}, respectively) was the lowest, whereas in TRP (72.9±25.4 and 48.0±22.5 mg WW m^{-3}, respectively) and SAP (550.9±85.8 and 240.3±42.3 mg WW m^{-3}, respectively) domains the values of this parameter were significantly higher (Fig. 2a, b).

Among the zooplankton, the abundance of copepods ranged from 67.0 to 1481.9 ind. m^{-3}, with an average value of 336.7±85.3 ind. m^{-3}; the biomass of copepods ranged from 28.4 to 694.4 mg WW m^{-3}, with an average value of 111.7±47.8 mg WW m^{-3}. These account for 82.8 and 86.3% of the total abundance and biomass of zooplankton, respectively. Therefore, the distribution of zooplankton was mainly determined by copepods. Among the three domains, 23 copepods species were identified for the STP domain, with their abundance ranging from 67.0 to 113.3 ind. m^{-3} and the biomass ranging from 28.4 to 33.7 mg WW m^{-3}. A total of 51 copepods species were identified for TRP domain, with the abundance ranging from 118.9 to 666.3 ind. m^{-3} and the biomass ranging from 16.2 to 80.3 mg WW m^{-3}; for the SAP domain, 23 copepods species were identified, with their abundance ranging from 334.3 to 1481.9 ind. m^{-3} and the biomass ranging from 88.8 to 694.4 mg WW m^{-3}. The dominant species for each domain are shown in Table.

Table. The average abundance (ind. m^{-3}), biomass (mg WW m^{-3}) of zooplankton and dominant species/taxa over the Emperor Seamounts.

Location	Domain: STP, Koko	Domain: TRP, Jingu	Domain: TRP, Nintoku	Domain: SAP, Suiko
Abundance±SD, ind. m^{-3}	129.2±38.4	212.6±51.3	346.8±67.2	843.5±89.2
The dominant species/taxa (order of dominance from greatest to least)	*Paracalanus aculeatus* *Oithona* spp. Fish eggs	*Paracalanus aculeatus* *Oithona* spp. Ostracoda	*Paracalanus aculeatus* Appendicularia *Oithona* spp.	*Oithona* spp. *Pseudocalanus newmani*
Biomass ±SD, mg WW m^{-3}	36.3±13.2	64.3±29.2	55.4±26.9	348.6±66.7
The dominant species/taxa (order of dominance from greatest to least)	*Metridia lucens* *Haloptilus acutifrons* *Euchaeta media* *Scaphocalanus magnus*	*Metridia lucens* *Eucalanus elongatus* *Pleuromamma gracilis*	*Eucalanus bungii* *Calanus pacificus* *Lophothrix frontalis*	*Neocalanus cristatus* *Pseudocalanus newmani* *Eucalanus bungii* *Metridia princeps*

Note: ''SD'' Standard deviation.

The diversity of zooplankton decreased with latitude (Fig. 2c, d). In TRP domain, the number of species and H' index were distinctly higher than those in STP and SAP domains. The peak values of the number of species and the H' index occurred over the Jingu Guyot (38°N). The TRP domain had the highest number of species, while the SAP domain showed the highest values of abundance and biomass.

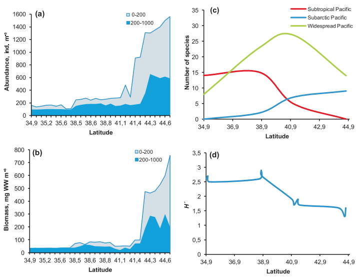

Fig. 2. Latitudinal variations in the abundance (a), biomass (b), number of copepod species of the zoogeographical groups (c) and Shannon-Wiener diversity index (H') (d).

Zooplankton composition and community structure

In the present study, 89 zooplankton taxa were identified. Among them, species from four genera of the order Amphipoda, seven genera of the order Pteropoda, 39 genera of the subclass Copepoda, and also larvae of benthic invertebrates and fish were identified. Of the 22 large taxonomic groups of zooplankton, copepods were the most important group in terms of species diversity, although some proportion of the animals found were not identified to a lower taxonomic level.

The zooplankton community structure within the area 170–171°E and 34–44°N over the Emperor Seamounts showed a significant latitudinal variation. A cluster analysis of the copepod community revealed a great similarity between the stations and only at a 78% similarity level three major grouping can be distinguished (Fig. 3).

The Subtropical Pacific community (Koko: 34–35°N) was characterized most distinctly by the presence of species of the Subtropical Pacific group, and the absence of species of the Subarctic Pacific group, and some species of the Widespread Pacific group.

The plankton was dominated by smaller-bodied tropical/subtropical copepods (*Corycaeus farranula*, *Harpacticus euterpina*, *Paracalanus aculeatus*, *Oncaea mediterranea*, *O. media*, *and* species of *Oithona).* There were also large-bodied tropical/subtropical copepods (*Euaugaptilus spp., Eucalanus elongatus*, *Haloptilus acutifrons*, *Lophothrix frontalis, and Rhincalanus nasutus*) which are well-known indicator species of the transformed warm waters of the North Pacific Equatorial Current (Fedosova, 1980). Among other copepods, we identified widely distributed oceanic species (such as *Metridia lucens* and *Scaphocalanus magnus*). The rest of the zooplankton groups (Cladocera, Amphipoda, Euphausiacea, Ostracoda, Siphonophora, Chaetognatha, Foraminifera, and Pteropoda) were not as diverse. Among the Pteropoda, we found species of the tropical genera *Atlanta*, *Carinaria*, and *Creseis*. Meroplankton was represented by larvae of Decapoda, Gastropoda, Polychaeta, Echinodermata, and Cirripedia.

The Transitional Pacific community (Jingu and Nintoku: 38–40°N) was characterized by a wide variety of species. The number of species of the Subtropical and Subarctic Pacific groups varied between stations in this area. Here, in the transitional waters, we recorded the largest number of zooplankton taxa and copepod species. The Jingu zooplankton communities showed a high taxonomic diversity, formed by species of tropical/subtropical and boreal genera that were not found further south (in the Subtropical Pacific domain). Here we observed the emergence of some tropical/subtropical copepods of the genera *Aetideus*, *Acrocalanus, Calocalanus, Centropages*, *Euchirella*, *Lucicutia* etc., Amphipoda (*Oxycephalus* and *Temisto*), Cumacea, Isopoda, and Pteropoda (*Diacria* and *Euclio*), and also the large-bodied boreal copepods *Eucalanus bungii and Neocalanus cristatus*. The area of Jingu Guyot was dominated by a mixed copepod fauna consisting of subtropical and subarctic Pacific species (*Scaphocalanus magnus*, *Pleuromamma gracilis*, *P. robusta*, *P. quadrungulata, Candacia bipinnata*, *Triconia conifera*, and *Oithona* spp.). The ratio of small- and large-bodied forms of copepods was almost even. In terms of species composition, the Nintoku community was mainly represented by large-bodied subtropical and boreal copepods (*Eucalanus bungii*, *Calanus pacificus*, *Neocalanus gracilis*, *N. crictatus*, *Paraeuchaeta barbata*, and *Pleuromamma xiphias*) and smaller-bodied species of *Paracalanus*, *Pseudocalanus*, *Oithona*, *Oncaea*, and *Harpacticus*. In contrast, this community included copepods of the boreal genera *Clausocalanus, Pseudocalanus*, and *Microcalanus* characteristic of subarctic waters (Brodsky, 1957). The diversity of tropical/subtropical copepods was significantly lower. Cephalopod larvae and colonial forms of salps, previously not found in the other domain, were observed north of the Nintoku summit.

The Subarctic Pacific community (Suiko: 44°N) showed further reduction in the diversity of Widespread Pacific group species, the absence of Subtropical Pacific group species, and an increased diversity of the Subarctic Pacific group species. Besides Subarctic copepods of *Eucalanus*, *Neocalanus*, *Metridia*, *Pseudocalanus, Oithona*, *Oncaea*, and *Triconia*, the indicator species of cold deep waters—*Euchaeta acuta*, *Paraeuchaeta barbata*, and *Pleuromamma robusta*—were also recorded from this area. The diversity of zooplankton taxa in the waters over Suiko Guyot significantly decreased, while the biomass increased tenfold compared to those in the areas of Koko, Jingu, and Nintoku guyots due to the predominance of large-bodied oceanic copepods.

The zooplankton community structure to strongly correlate with the environmental parameters was found. Strong positive correlations occurred between abundance of species from the Subtropical Pacific group and the values of temperature and salinity in the surface, and the temperature in the epipelagic zone, indicating an association to the Subtropical Pacific Water. In contrast, the abundance of the Subarctic Pacific group species showed a strong negative correlation with the values of temperature and salinity of the epipelagic zone, indicating a positive relationship with Subarctic Pacific Water.

In conclusion, the community structure of zooplankton showed a significant latitudinal variation in the vertical and horizontal distribution. Three major communities of zooplankton over the Emperor Seamounts were identified: a Subtropical Pacific community of subtropical and widespread species in an area within 34–35°N; a Subarctic Pacific community of subarctic and widespread species in an area within 41–44°N; and a Transitional Pacific community of subtropical, subarctic, and widespread species between 38 and 40°N. The average abundance and biomass of the communities increased towards higher latitudes: Subtropical < Transitional < Subarctic. The transitional area between the boreal and tropical zones in the northwestern Pacific Ocean has narrowed and ran between 38 and 40° N, as inferred from the data obtained. Ongoing climate change may shift the boundaries of the transitional zone between the "warm ocean" and the "cold ocean" and change the productivity of zooplankton communities, which necessitates regular monitoring of the unique pelagic ecosystems in the Northwest Pacific.